

**FIGURE 4** Geographical patterns of adaptive radiation imply the possibility of suppression between unrelated cichlid lineages. Two major phylogenetic lineages are responsible for most of the adaptive radiations of cichlid fish in African lakes, the tilapiines (black circles, three genera from top to bottom *Tilapia*, *Oreochromis*, *Sarotherodon*) and the *Astatotilapia*-related haplochromines (hatched circles; circle size represents number of species). Both groups are widely distributed across African lakes, and they often co-occur. However, they very rarely radiate in the same lake: In lakes in which haplochromines radiated, tilapiines did most often not, and most tilapiine radiations occurred in lakes from which haplochromines are absent. Reprinted with permission from Nature Publishing Group (Seehausen 2007).

eutrophication of Lake Victoria and the sudden boom in the 1980s of a large top predator, the Nile perch (*Lates niloticus*), introduced to the lake two decades before. The Nile perch depressed abundances of many cichlid species; the increased water turbidity made ecological specialization and behavioral reproductive isolation of coexisting cichlid species ineffective. The two effects together led to a sudden and rapid collapse of species diversity. Lake Victoria can be seen as a model in island conservation biology, where even localized human activities can have devastating effects on species diversity.

#### SEE ALSO THE FOLLOWING ARTICLES

Adaptive Radiation / Extinction / Freshwater Habitats / Lakes as Islands / Species–Area Relationship / Sticklebacks

#### FURTHER READING

- Genner, M. J., P. Nichols, G. Carvalho, R. L. Robinson, P. W. Shaw, A. Smith, and G. F. Turner. 2007. Evolution of a cichlid fish in a Lake Malawi satellite lake. *Proceedings of the Royal Society of London B* 274: 2249–2257.
- Genner, M. J., O. Seehausen, D. H. Lunt, D. A. Joyce, P. W. Shaw, G. R. Carvalho, and G. F. Turner. 2007. Age of cichlids: new dates for ancient lake fish radiations. *Molecular Biology and Evolution* 24: 1269–1282.
- Joyce, D. A., D. H. Lunt, R. Bills, G. F. Turner, C. Katongo, N. Duftner, C. Sturmbauer, and O. Seehausen. 2005. An extant cichlid fish radiation emerged in an extinct Pleistocene lake. *Nature* 435: 90–95.
- Kocher, T. D. 2004. Adaptive evolution and explosive speciation: the cichlid fish model. *Nature Reviews Genetics* 5: 288–298.
- Kwanabe, H., M. Hori, and N. Makoto, eds. 1997. Fish communities in Lake Tanganyika. Kyoto: Kyoto University Press.

- Rosenzweig, M. L. 2001. Loss of speciation rate will impoverish future diversity. *Proceedings of the National Academy of Sciences* 98: 5404–5410.
- Salzburger, W., T. Mack, E. Verheyen, and A. Meyer. 2005. Out of Tanganyika: genesis, explosive speciation, key innovations and phylogeography of the haplochromine cichlid fishes. *BMC Evolutionary Biology* 5: 17.
- Schliewen, U., and B. Klee. 2004. Reticulate sympatric speciation in Cameroonian crater lake cichlids. *Frontiers in Zoology* 1: 1–12.
- Seehausen, O. 2006. African cichlid fish: a model system in adaptive radiation research. *Proceedings of the Royal Society of London B* 273: 1987–1998.
- Seehausen, O. 2007. Chance, historical contingency and ecological determinism jointly determine the rate of adaptive radiation. *Heredity* 99: 361–363.
- Stager, J. C., and T. C. Johnson. 2008. The Late Pleistocene desiccation of Lake Victoria and the origin of its endemic biota. *Hydrobiologia* 596: 5–16.

## CLIMATE CHANGE

DAVID A. BURNEY

National Tropical Botanical Garden, Kalaheo, Hawaii

Climate changes are well documented for islands throughout the world on many scales, from hundreds of millennia to recent decades. These changes in temperature and moisture have had large effects on many other ecological factors, including sea level, coastal dynamics, biogeography, extinctions, and human culture. Climate changes on islands have varied in severity according to the size of the island, its latitude and elevation range, and the effects of human activities. Climate changes predicted for the near future can be expected to have drastic effects on all islands, even to the point of destroying some island ecosystems, challenging human lifeways and culture, and driving extinction events. Some low islands may disappear entirely if global warming–driven sea-level rise is as great as predicted by some models.

#### PAST CLIMATE CHANGE

##### Global Effects on Island Climate

Paleoclimatologists have revealed that global climate is always changing. These scientists have used evidence from sediments, stable isotopes, and microfossils to show that, in the deep-sea sediments, ice cores, and lake deposits they have studied, there is abundant evidence that earth's climate at all latitudes has gone through roughly 20 glacial-interglacial cycles over the last 2 million years. The strongest cycle is approximately 100,000 years in duration, but superimposed on this pattern are other cycles at approximately 20,000 and 40,000 years, all

apparently driven by variations in the earth's orbit and tilt (Fig. 1). Complex feedback mechanisms in the earth's many climatic variables have resulted in a series of ice ages, each several tens of millennia in length, interspersed with briefer warm interglacial intervals of 10 to 20 millennia, such as our present Holocene period, which has lasted for about 11,000 years. These global trends have had some drastic effects on islands. For instance, on very large, high islands such as Madagascar and New Guinea, full ice-age conditions drove the tree line on mountains down about 1000 m in elevation, such that large areas of these tropical islands were too cold to support tropical forest over large areas. Islands with very high mountains, such as the Big Island of Hawaii, had alpine glaciers despite their tropical latitude. Under these cooler regimes, some lowland areas were much drier than they are today, with the resultant spread of savanna vegetation. Conversely, during interglacials such as the present Holocene, forest has spread over large areas of many tropical islands.

For islands in particular, these glacial-interglacial vicissitudes of climate may have another drastic consequence: During glacial maximum, the coldest time of an ice age, so much water is locked up in the polar caps and conti-

ental glaciers that sea level is lowered by 120 m or more. For an island group such as the Bahamas, this means that today's relatively small islands coalesce into a few quite big islands—at times during the Pleistocene, the Bahamas have been about ten times their present area. This growing together of islands has profound biogeographic effects. The flora and fauna of Maui, Lanai, Kahoolawe, and Molokai in the Hawaiian Islands has more similarity than those of other islands in the chain, likely because they formed one large island during low Pleistocene sea stands.

### Local Effects on Island Climate

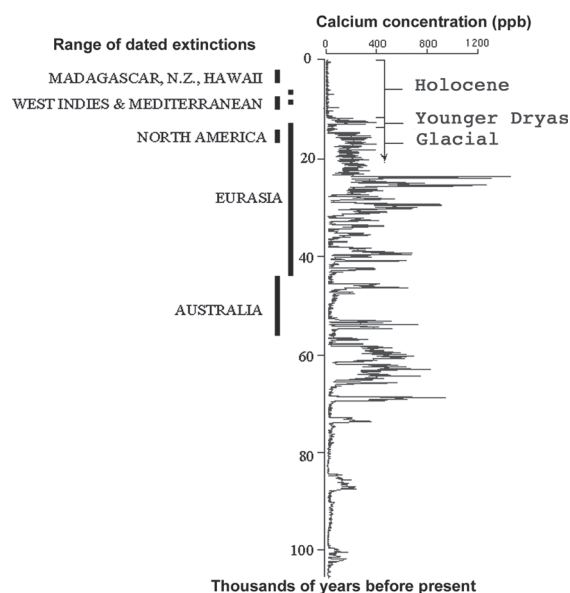
On more recent time scales, climate has changed on islands primarily through the effects that humans have had on the local ecology. Although difficult to measure, the large-scale deforestation that has occurred since human arrival to remote islands has reduced rainfall, increased runoff, and allowed the soils of these sites to heat up. Famous extreme examples are New Zealand, Madagascar, and Rapa Nui (Easter Island), where much of the original forest cover has been lost, and changes in the local microclimate have hindered reforestation efforts.

A debate has raged in the scientific community regarding the role of “natural” and human-caused climate change in the catastrophic extinctions that have been documented for many of the world's islands. Unique faunas have lost much of their diversity over millennial time scales, challenging scientists to explain this powerful trend. A look at the major variations in global climate, plotted alongside these major extinction events, however, shows that most island extinctions have coincided not with glacial-interglacial cycles but with the advent of humans to these systems (Fig. 1). This pattern holds for the islands reached earliest by humans (Australia and New Guinea, perhaps 50,000 years ago), continues through the Mediterranean and Caribbean islands reached in the mid-Holocene, and culminates with those islands reached last, such as Hawaii, Madagascar, and New Zealand in late prehistoric times and the Mascarenes and Galapagos in the historical period.

Thus, despite the drastic effects of climate change on sea level, coastal dynamics, biogeography, and many other island factors, it has ultimately been humans, not climate, that have changed islands most.

### FUTURE CLIMATE CHANGE

One sad irony of modern life is that humans are now showing their capability to modify climate not only locally, but perhaps also on a global scale. There is virtual unanimity among climatologists that global warming is not just a real threat in the future but is in fact happening now. Events



**FIGURE 1** A high-resolution calcium concentration record from the GISP2 Greenland ice core indicating the relative amount of atmospheric dust, an index for cool and dry (long horizontal bars) versus wet and warm conditions (much shorter bars). Note that the interglacial-type climate, such as in the present Holocene, is generally warmer and wetter globally than the typical late Pleistocene full-glacial climate, which was cooler and drier in many locations. This indirect measure of the extent of vegetative cover, as well as other Pleistocene climatic indices, shows no correlation with the distribution of “last occurrence” dates for extinct island fauna or continental extinctions (vertical bars). From Burney and Flannery 2005.

detected in the fossil record may now repeat themselves on an accelerated time scale. The well-documented melting of the polar ice caps and alpine glaciers is causing sea level to rise, threatening coastlines with erosion, flooding coastal wetlands, and inundating low atoll islands. Island countries such as the Maldives and many of the islands of Micronesia, where elevations scarcely exceed 2 m, may virtually disappear in coming decades if the model predictions for sea level rise in a CO<sub>2</sub>-enriched world prove true. Island nations may soon be faced with the prospect of thousands or even millions of environmental refugees.

Just as in prehistoric times, warming will drive cool-adapted island species higher up the mountains, but many such species may go extinct if the island lacks sufficient area at high elevations to accommodate them. Range shifts in response to climate change on islands today are further complicated by the fact that the mid-elevations and highlands of many islands are already heavily populated and transformed by humans.

Cloud forests and other upper-elevation wet zones, which harbor the richest diversity of endemic species on some islands, may be particularly affected by global climate change. Paleoclimatological data for Maui, for instance, suggest that climatic warming may raise the mean elevation of the base of the cloud bank, thus reducing or completely eliminating these cloud forest habitats on small islands that lack large areas of high elevation.

Another worrisome consequence of future climate change for islands is the predicted increase in extreme weather events. Because of their smaller land area and exposure to marine influences, islands are especially vulnerable to increased frequency and violence of storms, a well-supported prediction from climatological studies of the effects of increased ocean temperature on tropical storm formation and other extreme marine events. Adding further to the climatic uncertainty is the apparent correlation between warmer oceans and the frequency and severity of El Niño–Southern Oscillation (ENSO) events and other large-scale feedback connections between ocean and atmosphere.

The predicted increase in uncertainty in climate patterns may be a special problem for islands, as floods, droughts, and heat waves pose great challenges to the stability of agriculture, fisheries, and other human enterprises on islands, as well as the native biota. Tropical island forests have declined in some areas due to severe droughts. For instance, in the past decade, vast areas of rain forest in Borneo dried out and burned during a drought apparently related to a “Super-ENSO” event.

Increased storminess, wildfires, and rising temperatures have been observed to have synergistic effects on another

great challenge to the biota of islands—biological invasions. Many of the alien imports that are driving island species to extinction and interfering with agriculture on islands throughout the world are favored by increased disturbance from hurricanes and other climatic extremes. In this way, even the world’s most remote islands share a fate with the large, developed land masses of the planet, because the human-wrought changes to the atmosphere affect the climate everywhere.

#### SEE ALSO THE FOLLOWING ARTICLES

Climate on Islands / Deforestation / Global Warming / Invasion Biology / Sea-Level Change

#### FURTHER READING

- Burney, D.A., and T.F. Flannery. 2005. Fifty millennia of catastrophic extinctions after human contact. *Trends in Ecology and Evolution* 20: 395–401.
- Burney, D.A., R.V. DeCandido, L.P. Burney, F.N. Kostel-Hughes, T.W. Stafford, and H.F. James. 1995. A Holocene record of climate change, fire ecology, and human activity from montane Flat Top Bog, Maui. *Journal of Paleolimnology* 13: 209–217.
- Burney, D.A., L.P. Burney, L.R. Godfrey, W.L. Jungers, S.M. Goodman, H.T. Wright, and A.J.T. Jull. 2004. A chronology for late prehistoric Madagascar. *Journal of Human Evolution* 47: 25–63.
- Graham, M.H., P.K. Dayton, and J.M. Erlandson. 2003. Ice-ages and ecological transitions on temperate coasts. *Trends in Ecology and Evolution* 18: 33–40.
- Mayewski, P.A., L.D. Meeker, S. Whitlow, M.S. Twickler, M.C. Morrison, P. Bloomfield, G.C. Bond, R.B. Alley, A.J. Gow, D.A. Meese, P.M. Grootes, M. Ram, K.C. Taylor, and W. Wumkes. 1994. Changes in atmospheric circulation and ocean ice cover over the North Atlantic during the last 41,000 years. *Science* 263: 1747–1751.
- Rizvi, H. 2007. Climate change: leaders sound the alarm on island peoples, economies. <http://ipsnews.net/news.asp?idnews=37525>.
- Shackleton, N.J., and N.D. Opdyke. 1973. Oxygen isotope and palaeomagnetic stratigraphy of equatorial Pacific core V28-238: oxygen isotope temperatures and ice volumes on a 10<sup>5</sup> year and 10<sup>6</sup> year scale. *Quaternary Research* 3: 39–55.

---

## CLIMATE ON ISLANDS

THOMAS A. SCHROEDER

*University of Hawaii, Manoa*

Climate is the average of weather conditions over a long period of time. The period is at least 30 years. The standard weather parameters considered are temperature and precipitation, which are primary controls on distributions of vegetation. In addition to the average conditions, the variance of these conditions is equally important. Year-